METASQUALODON HARWOODI (SANGER, 1881)—A REDESCRIPTION

By NEVILLE S. PLEDGE* AND KARLHEINZ ROTHAUSEN†

ABSTRACT

PLEDGE, N. S. & ROTHAUSEN, K., 1977: *Metasqualodon harwoodi* (Sanger, 1881)—a redescription. *Rec. S. Aust. Mus.* 17 (17): 285-297.

The long-lost holotype and several undescribed paratype teeth of the squalodontid whale *Metasqualodon harwoodi* have been rediscovered, and form the basis for a more detailed description. Comparison is made with the teeth of other squalodontids from Australia and New Zealand, and based on Rothausen's revision of European Squalodontidae, an attempt is made to classify *Metasqualodon* more precisely. The teeth represent a valid genus.

General tendencies in the evolution of squalodontid teeth make it more likely that *Metasqualodon* is nearer to the evolutionary stage of longirostral Lower Miocene species of *Squalodon* in the Northern Hemisphere than to that of presently known brevirostral genera of the Southern Hemisphere. Nevertheless, curvature of the crown and roots, and the denticles on the anterior-most buccal tooth indicate that the teeth probably belong to a brevirostral form. This would mean that there was a tendency in the evolution of the teeth of brevirostral squalodontids similar to that shown in the longirostral forms of Europe.

In any case, this gives a supplementary indication to the disputed age of the find since, on the grounds of preservation, it has been determined as coming from the uppermost part of the Ettrick Formation, and is therefore very late Oligocene.

INTRODUCTION

In 1880, Sanger (1881) reported to the Linnean Society of New South Wales the discovery of a tooth and some fragments of a second at Wellington, South Australia. These he regarded as belonging to a new zeuglodont whale species "*Zeuglodon harwoodii*". He figured and described a "molar" tooth, consisting of a near-complete serrated crown and the upper, confluent part of the roots.

Later, Hall (1911), in discussing the systematic positions of *Squalodon* and "*Zeuglodon*" from Australia, compared "*Z.*" *harwoodi* and *Squalodon wilkinsoni* McCoy (1867), and put both into new genera: viz. *Metasqualodon harwoodi* (Sanger) and *Parasqualodon wilkinsoni* (McCoy). His treatment of *M. harwoodi* was necessarily only cursory and based on Sanger's rather inadequate paper, because the whereabouts of the type material was unknown.

In 1948, Charles Fenner, then Honorary Curator of Fossils at the South Australian Museum, discovered a box of teeth recorded as P8446 in the Palaeontological Register, and stored as a holotype. The box contained six teeth or fragments thereof, glued to a card labelling them as molars and canines. Two of the "molars" were also labelled as types. In addition, a slip bearing the legend (in script):

Zeuglodon teeth	
(Notodanus tooth)	separated
	100[r]
Wellington	
J. C. Harwood	
Sydnam	Norwood

and a cutting of the text figures from Sanger's paper were enclosed. Fenner realised that this box contained Sanger's type material and more besides. The pencilled addition "separated" referred to the "*Notidanus*" tooth, which was not present in the box. This tooth was later discovered (1972) elsewhere in the collection, and bears the additional information on its card:

> "Fossil shark tooth, Notidanus sp?
> River Murray Cliffs near Wellington, S. Austral.
> pres. by Mr. J. C. Harwood, December 1881."

The tooth is additionally labelled "*Notidanus primigenius*".

However, the whereabouts of *Zeuglodon harwoodi* was not disclosed for some time, for it was not seen by Flynn (1948) when he minutely described the nearly complete skull and mandibles of *Prosqualodon davidi* Flynn; nor was it seen by Glaessner (1955) when he established *Squalodon gambierensis*, although he later rediscovered it.

Rothausen (1968: pp. 85-86) established a terminology and some indices to standardise the description of squalodontid whales. Appendix

* South Australian Museum, Adelaide, South Australia, 5000.

† D-6500 Mainz, Geowissenschaftliches Institut der Universität, Saarstr. 21, Federal Republic of Germany.

8th August, 1977

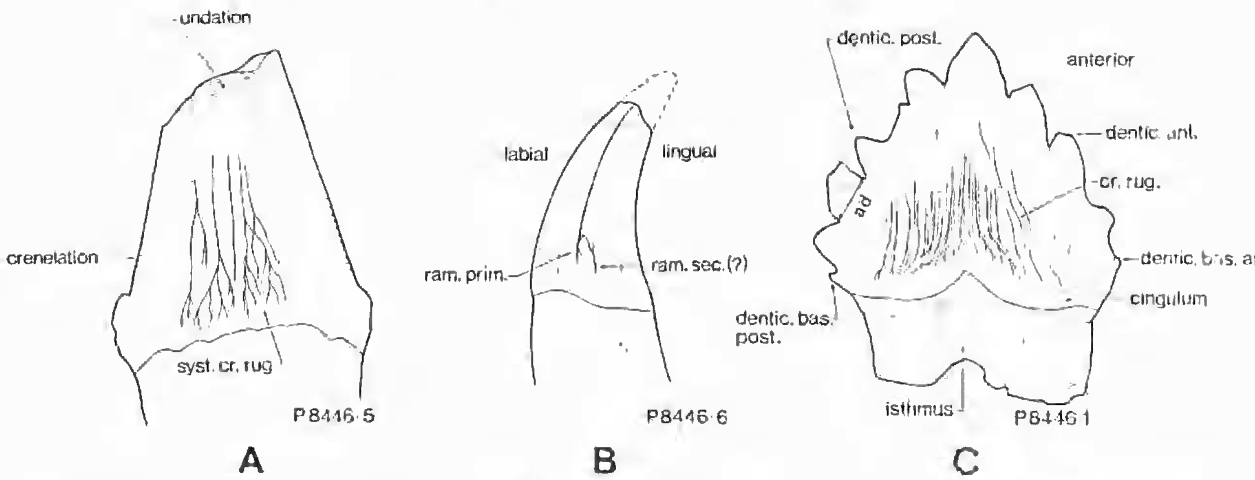

Fig 1. Feature terminology in Squalodontoid teeth. Diagrams not to scale. A. Internal face of P8446.6, diagramatically showing crenelation, syst. cr. rug. and undation. B. Anterior view of P8446.5, showing basal region of anterior carina with ram. prim. and possible ram. sec. C. Lingual view of P8446.1, showing anterior and posterior denticles, and dentic. bas. ant. and post., syst. cr. rug., and cingulum.

1 gives a summary of this terminology, with additional terms used herein. A number of them are commonly applied in the text as Latin abbreviations. See Fig. 1.

HISTORY OF STUDIES ON AUSTRALIAN AND NEW ZEALAND SQUALODONTIDS

Flynn (1948: p. 185) gave a precise and concise account of discoveries of and papers on Australasian archaeocetes and primitive odontocetes, therefore only the time from 1948 till now shall be considered except for a few references not mentioned by him.

1939. Pritchard describes a partial skull and jaws of a new whale *Mammalodon pritchardi*. The preserved teeth are extremely worn, to the extent that comparison with other squalodontoid teeth is not possible.

1942. Camp and Kellogg (in Camp 1942: p. 367) agree with Thomson (1905: p. 491) in contrast to Benham (1935a: p. 238) (who thought it a reptile as accepted by Neave 1940 (*b*): p. 395 in wrong spelling "*Tangarosaurus*"), that *Tangaroasaurus kakanuiensis* Benham, 1935 represents the rostrum of a squalodontid; accepted also by Romer (1945: p. 624; 1966: p. 392) and Dechaseaux (1961: p. 860) both in wrong spelling (*Taugarasaurus*), and by Rothausen in his revision (1965: pp. 656-658), who could verify it in detail.

1948. Flynn published a full description of the near complete skull of *Prosqualodon davidi* Flynn, 1923 discovered by him at Wynyard, Tasmania, in September 1919 (*vide* Mahoney and Ride 1975: pp. 161-162). He first mentioned it in 1920 and described and named it in 1923. An addendum by Carter (in Flynn 1948: pp. 192-193) gives a microscopic comparison of the enamel structure of *P. davidi*, "*Zeuglodon*" *osiris*, several carnivores, a creodont, and an ungulate (*Sus*). The two whales show a closer affinity to the ungulate than to any carnivore. Flynn here discusses also—with other odontocetes—the position of *Metasqualodon harwoodi*.

1948. Sanger's type material is rediscovered in Adelaide, but its importance is not fully realised, and its whereabouts are not made known immediately.

1955. Glaessner describes a buccal tooth, probably a lower right, found in Oligocene bryozoal limestone at Mt. Gambier. It is of a form not previously recorded from Australasia, and is given the name *Squalodon gambierense*. (Fig. 3M,N).

1961. Rothausen discusses the position of "*Microcetus*" *hectori* Benham 1935 (*b*) and he is sure that it at least belongs in another genus than the genotype *M. ambiguus* (v. Meyer, 1840).

1964. Dickson describes *Prosqualodon marplesi* Dickson 1964 from Upper Oligocene beds in New Zealand.

1965. Rothausen in a revision of European squalodontids also discusses the non-European forms in some detail. This part of his manuscript is not yet published, even in abstract form.

1970. Rothausen discusses general aspects of some Squalodontoidea from Australia and New Zealand in connection with the question of the Oligocene-Miocene boundary.

1972. Climo and Baker present an updated summary of studies on New Zealand squalodonts and describe a new genus and species *Austrosqualodon trirhizodonta* based on a pair of edentulous mandibles collected in 1970 in Duntroonian (Middle Oligocene) siltstone near Nelson, New Zealand. The genus is considered by these authors to be allied to *Squalodon* Grateloup, but differs in having a small median third root on the molariform teeth.

1972. Glaessner redescribes a cetacean tooth from New Zealand, previously described by Davis (1888) as *Squalodon serratus*. It is from the same stratigraphic horizon as *Kekenodon onomata* Hector 1881 and shows some similarities with, but is considerably smaller than, that species. Glaessner also to some extent clarifies the rather uncertain situation concerning isolated teeth of squalodontoids in the Australian-New Zealand area.

1973. Keyes describes, but does not name, two buccal teeth of a "protosqualodontid" from the Lower Oligocene of Oamaru, New Zealand. He also revises the records of all known fossil Cetacea from New Zealand.

1975. Mahoney and Ride, indexing the genera and species of Australasian fossil mammals, list fifteen species of fossil cetaceans, and *inter alia* note that the type of *Metasqualodon harwoodi* had disappeared and that the cranium and much of the skeleton of the type of *Prosqualodon davidi* Flynn had been lost in 1961 during renovations of the Zoology Department, University of Tasmania.

1976. Whitmore and Sanders review the Oligocene Cetacea, but do not mention *Metasqualodon*, apparently believing it to be a Miocene species.

In this present paper, a summary of the stratigraphic occurrences of the squalodonts of Australia and New Zealand, in the light of current knowledge and interpretation, is given in Table 1. This has been done in more detail for New Zealand species by Keyes (1973).

TABLE 1
STRATIGRAPHIC DISTRIBUTION OF AUSTRALASIAN SQUALODONTOIDEA

Species	Locality	Formation	Age	Age Reference
Tangaroasaurus kakanuiensis Benham, 1935a	Kakanui, Otago, N.Z.	Blue clay	Otaian-Altonian (Early to Middle Miocene) or Waitakian (Late Oligocene)	Keyes (1973) Climo and Baker (1972)
Prosqualodon davidi Flynn, 1923 ..	Fossil Bluff, Wynyard, Tas.	Fossil Bluff Sandstone	Early Longfordian (very early Miocene)	Ludbrook (1973)
Metasqualodon harwoodi Sanger 1881	Near Wellington, River Murray, S.A.	Ettrick Formation..	Janjukian (Late Oligocene)	This paper
Parasqualodon ? wilkinsoni McCoy 1867	Castle Cove, Loc. AW3, Aire Coast, Vic.	Calder River Limestone	Janjukian (Late Oligocene to earliest Miocene)	Carter (1958) Ludbrook (1973)
Squalodon ? andrewi Benham 1942	Clarendon Limestone Quarry, Otago, N.Z.	—	Waitakian (Late Oligocene)	—
"*Prosqualdodon*" *hamiltoni* Benham 1937	Caversham Quarry, Dunedin, N.Z.	Caversham Sandstone	Waitakian (Late Oligocene)	—
Prosqualodon marplesi Dickson 1964	Near Trig. Z, Waitaki Valley, Otago, N.Z.	Waitoura Marl Member of Otekaike Limestone	(Late Oligocene)	—
"*Microcetus*" *hectori* Benham 1935b	Maerewhenua River, Waitaki Valley, Otago, N.Z.	Maerewhenua Glauconitic Limestone Member of Otekaike Limestone	Waitakian (Late Oligocene)	—
Austrosqualodon trirhizodonta Climo and Baker 1972	S.E. of Fossil Point, N.W. Nelson, N.Z.	Glauconitic Sandstone	Duntroonian (Middle Oligocene)	Keyes (1973)
Squalodon ? gambierensis Glaessner 1955	Pritchard's Quarry Mount Gambier, S.A.	Gambier Limestone	Early "Janjukian" (Early Middle Oligocene)	Jenkins (1974) p.292
Squalodon ? serratus Davis 1888 ..	Karetu River, North Canterbury, N.Z.	Weka Pass Stone	Whaingaroan-Duntroonian (Early Middle Oligocene)	Glaessner (1972)
Unnamed squalodontoid	Gay's Limestone Quarry, Weston, Oamaru, N.Z.	McDonald Limestone	Whaingaroan (Early Oligocene)	Keyes (1973)

TAXONOMY

Squalodontoidea Simpson, 1945
Squalodontidae Brandt, 1873
Squalodontinae Rothausen, 1968

Metasqualodon Hall, 1911

Metasqualodon harwoodi (Sanger 1881)

Zeuglodon Harwoodii Sanger 1881: 298-300, Fig. A, B.

Zeuglodon Harwoodi Sanger Stromer 1908: 147.

Metasqualodon harwoodi (Sanger) Hall 1911: 257, 262, 263, pl. 36, Fig. 7A, B (not Fig. 6).

Microzeuglodon ? Harwoodi (Sanger) Abel 1913: 220.

Zeuglodon harwoodi Sanger Abel 1913: 209.

S. harwoodi Sanger Winge 1919: 129.

Metasqualodon harwoodi (Sanger) Kellogg 1923: 20, 40.

Zeuglodon harwoodi Pritchard 1939: 153, 155.

Metasqualodon Hall 1911 Neave 1940: 133.

Metasqualodon harwoodi Flynn 1948: 186.

Metasqualodon harwoodi Glaessner 1955: 336.

Metasqualodon Hall 1911 Rothausen 1958: 372.

Metasqualodon (="*Zeuglodon*") *harwoodi* Thenius 1959: 273.

Metasqualodon harwoodi (Sanger 1881) Rothausen 1965: 659.

Metasqualodon harwoodi Rothausen 1970: Fig. 1.

Metasqualodon Hall 1911 Dubrovo 1971: 89.

Metasqualodon harwoodi Sanger Climo and Baker 1972: 61.

Metasqualodon harwoodi (Sanger) Glaessner 1972: 185.

Metasqualodon Keyes 1973: 384.

Metasqualodon harwoodi Mahoney and Ride 1975: 158.

Zeuglodon harwoodi Sanger *idem*: 164.

Holotype: A buccal tooth lacking only the distal parts of the roots, some points of the crown and part of the enamel at the labial face (Fig. 3A-B; Sanger 1881: p. 298, Fig. A-B). South Australian Museum, Adelaide P8446.1.

Paratypes: Five teeth or fragments of teeth (Fig. 3C-J). South Australian Museum, Adelaide P8446.2-6.

Type Locality: The teeth were found near Wellington, on the River Murray in South Australia (Fig. 2). ". . . in a bed of yellow calcareous clay, containing specimens of *Echinus, Spatangus, Clypeaster, Pecten, Turritella, Corbis* and *Spondylus*." (Sanger 1881: p. 298). These accompanying fossils have been lost, so their modern identities are unknown.

Age: Late Oligocene (see discussion below).

Diagnosis: Typical squalodontoid teeth with the following characteristics:

Posterior buccal teeth with many dentic. ant. and dentic. post. including dentic. bas. ant. and post. on antero-posterior carina. Labial face shows only few weak cr. rug., the lingual face stronger. Characteristic number of cr. rug. about 14-15, ID with 18.6 is small. Low values for ant.-post. diameter of crown base, middle value for apical-angle, and not a very high degree of symmetry. Root with two fangs, confluent at top by thin isthmus extending for up to 10 mm (estimated) but often less in more posterior buccal teeth.

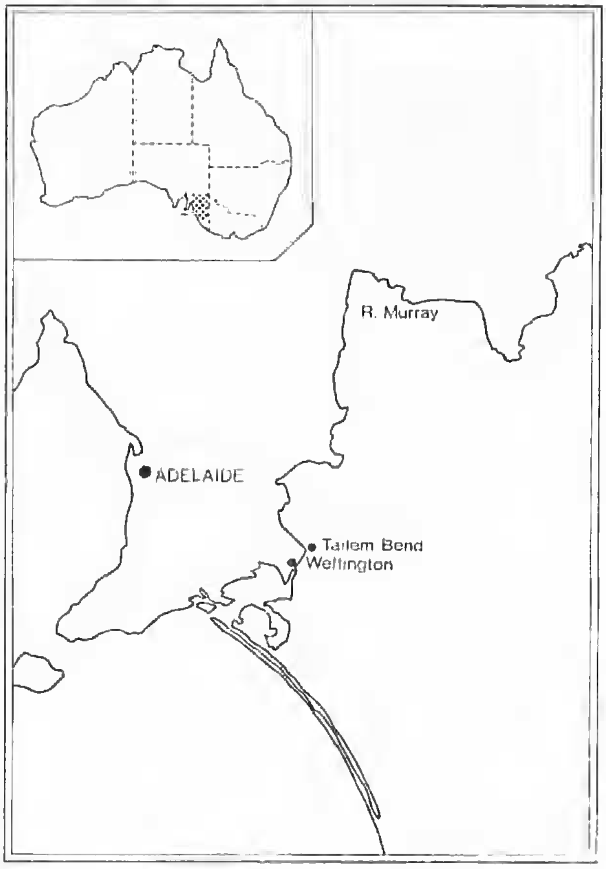

Fig. 2. Locality map.

Cheek teeth of more anterior position are similar but with fewer denticles and longer isthmus.

The anterior-most cheek teeth show one or two denticles.

Redescription of Holotype: The Holotype (P8446.1; Fig. 3 A, B) is a well preserved buccal tooth which lacks most of the roots, the points of several denticles, and part of the enamel from the labial face. The crown is laterally compressed, triangular in facial aspect, with a distinct antero-posterior carina which is occupied with a number of well-defined, acutely-pointed denticles: three dentic. ant. and one dentic. bas. ant. as well as five dentic. post. and one dentic. bas. post. The dentic. bas. on each side is very small, and others are about the same size, somewhat smaller than the apical point. All denticles bear an antero-posterior carina.

The greatest length of this buccal tooth is above the base of the crown, at the level of the apices of the dentic. bas. Greatest width is in that part of the crown above the anterior root. The base of the enamel is visible only on the lingual face, and is straight except for a median V-shaped embayment. Both faces show a wide "sulcus" in this position, which corresponds to the junction between the two roots.

The labial face bears faint, near-vertical cr. rug. which appear to converge near the apex, some also diverging to enter the denticles. The enamel of the lingual face is more strongly decorated: above a smooth basal zone (the cingulum) up to 4 mm wide, irregular stronger cristae rugae converge near the apex, some also diverging to enter the denticles. The cristae are most pronounced at their lower ends where they have developed small tubercular prominences bordering the cingulum, above which they are papillated, especially those of the posterior part of the crown. The cr. rug. die out without reaching the apex.

In anterior profile, the crown is more convex on the labial face, but this only concerns the anterior part of the crown. The apical part is slightly incurved. The enamel is thickened at the base to form a smooth cingulum.

The two roots are broken off about 6-7 mm below the crown. The anterior root is circular in section, the other is laterally compressed. The fracture shows the radial structure of the dentine, and shows that the pulp cavities of the two roots join within the thin isthmus which connects the proximal portion of the roots. Irregular, deep, vertical striations are seen on the parts of the roots nearest to the base of the crown, particularly on the labial face.

Most characters and indices (Table 2) are in good accordance with B^{9-10} dext. of European Squalodontinae, but with very small absolute dimensions.

TABLE 2

DIMENSIONS OF HYPODIGM TEETH OF *METASQUALODON HARWOODI*

	Holotype	Paratypes				
	P8446.1 post.B sup.?	P8446.2 post.B fragm.	P8446.3 post.B inf.? fragm.	P8446.4 mid.B sup.?	P8446.5 mid.B sup.?	P8446.5 ant.B sup.?
(1) Max. ant.-post. diameter of crown ...	22·8	?	?	~17·5	11·9	8·6
(2) Ant.-post. diameter at base of crown (*a*)	20·4	?	?	~17·5	11·2	8·5
(3) Apical-angle	55	?	?	>47	33°	~31°
(4) Lat. diameter at base of crown (ant. in two-rooted teeth); (*b*)	8·8	?	?	>7·8	7·6	7·1
(5) Lat. diameter at base of post. part of crown in two-rooted teeth	7·2	?	?	>7·6	—	—
(6) Number of dentic. ant.	4	4	?	1	1	1
(7) Number of dentic. post.	6	?	?	2	1	0
(8) Ant.-post. diameter of largest dentic post. (*ad*)	3·8	?	?	5·7	~3·4	—
(9) Index dentic. (in %)	18·6	?	?	—	—	—
(10 Characteristic number of cr. rug......	14/15	?	?	—	—	—
(11) Vertical width of cingulum in the preserved parts	~4	>2	~4	~3	~1·1	~1·7
(12) Index bas. (in %)	43·1	?	?	44·6	67·8	83·5
(13) Number of roots	2	2	2	2	1	1
(14) Extent of isthmus	>9	~8·5	>6·4	>10	—	—
(15) Max. lat. diameter of ant. root or single root	7·8	~8	?	~8·5	8·2	7·8
(16) Max. lat. diameter of post root	6·6	?	?	~7·5	—	—

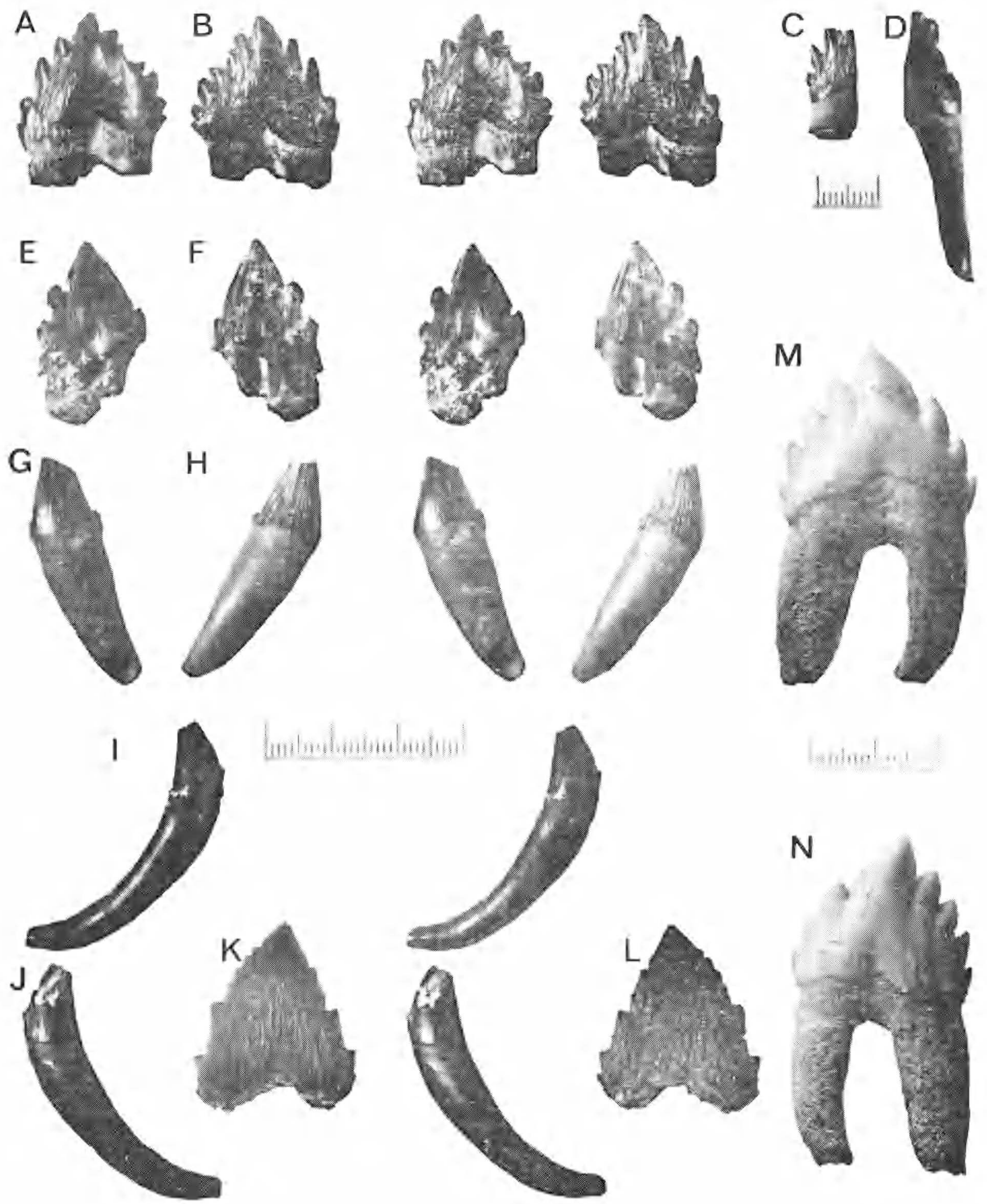

Fig. 3. A-J, the hypodigm teeth of *Metasqualodon harwoodi* (Sanger 1881). A. P8446.1, labial face; B. ditto, lingual; C. P8446.2, lingual; D. P8446.3, lingual; E. P8446.4, labial; F. ditto, lingual; G. P8446.5, labial; H. ditto, lingual; I. P8446.6, labial; J. ditto, lingual; K. *Prosqualodon davidi* Flynn, AUGD T857, labial; L. ditto, lingual; M. *Squalodon ? gambierensis* Glaessner, AUGD F15107, labial; N. ditto, lingual face. All approximately natural size. A, B, E-J stereophotos and to the same scale.

Description of Paratypes: Sanger (1881: p. 298) mentioned a fragment of a second tooth in his original description. One fragment in the assemblage is labelled "type", and consists of the anterior internal quarter of a cheek tooth, lacking the apex and most of the root (P8446.2; Fig. 3 C).

Its features are similar to those of the holotype, but it displays some better. Three dentic. ant. are present or indicated, and also a very small dentic. bas. ant. All are sharply pointed, and separated by deep grooves. The cr. rug. are very strongly developed, producing sharp-crested ridges converging towards the apex. A smooth 2 mm high cingulum borders the root.

Only a few millimetres of root are present, but it has a roughly circular section, and is deep enough to indicate that the isthmus joining the roots did not extend very deeply—only 7·5 mm below the medial base of the crown enamel.

It is not possible to say more than that its position is middle or posterior buccal.

Another buccal tooth originally labelled as "canine tooth", is represented by the posterior internal quarter of the crown, and most of the posterior root (P8446.3; Fig. 3 D). It is not part of the tooth represented by the foregoing fragment. The preservation of the crown is poor; only the apex and the topmost dentic. post., or, more likely, only the two topmost dentic. post., are present with their lingual parts, and both lack apices through wear or damage; the cr. rug. are relatively course, but appear worn. The cingulum is 3-4 mm high.

The strongly incurved root is nearly complete, lacking only a short proximal portion and the labial part nearest to the crown, so exposing the pulp cavity. The isthmus is short, about 6-7 mm. In lateral view the root is straight.

This latter characteristic is typical for lower buccals in European squalodontids and thus we probably have a fragment of a B inf. dext. of middle or posterior position.

A more anterior cheek tooth is represented by a near-complete crown with a small portion of its root (P8446.4; Fig. 3 E, F). The crown is laterally compressed, is high-triangular in side view, and slightly incurved in profile. The antero-posterior carina bears one dentic. ant., near the base of the crown, and two widely spaced dentic. post. Small basal denticles may have been present, but are not preserved. The labial face is mainly smooth, having a few short, poorly developed cr. rug. near the base posterior to the median sulcus. The enamel of the lingual face is preserved only in the anterior half, and shows strong irregular cr. rug.

The root is preserved, poorly, only on the lingual side. The two roots are seen to be confluent, but the extent of the isthmus cannot be determined. The pulp cavity is obscured by matrix.

In most quantitative characteristics (Table 2) and in the general appearance, it is similar to a left B^6 in European squalodontids, but with smaller absolute dimensions.

Two teeth, originally labelled as canines, we deem to be anterior-most buccal teeth.

The larger is a specimen lacking the crown apex and the distal portion of the single root (P8446.5; Fig. 3 G, H). The crown is a laterally compressed cone, incurved, with a pronounced antero-posterior carina. A small dentic. bas., with apex missing, is present at each end of the carina, and minute denticulations can just be perceived along the lingual side, a phenomenon in all anterior teeth of squalodontids for which one of the authors proposed the term "crenelation" (Fig. 1 A; Rothausen 1965: p. 26, Abb. 1). The labial face is convex, and smooth except for a few short, poorly developed cr. rug. near the middle and in the posterior half. The lingual face is concave in profile and is strongly decorated with cr. rug. converging in the direction of the apex. The systems of cr. rug. die out in a narrow smooth cingulum in which the enamel is not thickened. The root is somewhat tumid just below the crown, and is laterally compressed there. More distally it narrows and becomes circular in section.

Most of its characteristics and indices, except its smaller absolute dimensions, are similar to those of a B^4 dext. of European squalodontids. But there are some differences in habitus. For example, in European forms no tooth anterior to $B^5/_5$ has any dentic. ant. or bas. ant.

An upper buccal tooth is especially indicated here by a character that seems common to all anterior teeth of squalodontids—the carina divides into a main branch (ramus primus = ram. prim.) and another, weaker one (ramus secundus = ram. sec.) at its basal anterior part, and as far as it was possible to check this character, the ram. sec. branches off to the lingual side in upper teeth and to the labial side in lower teeth. (Fig. 1 B; Rothausen 1965,

Abb. 21-28, 53-56). Here it branches off to the lingual side.

The sixth specimen is more complete and smaller, and from the opposite jaw or mandible (P8446.6; Fig. 3 I, J). Its identity is uncertain, as it shows the great length and curvature of root associated with canines and third incisors of squalodontids, and yet bears a distinct dentic. ant. near (4·7 mm) the anterior end of the carina. Although there are, in other squalodontids, similar teeth which belong to the most anterior of the buccal series, nevertheless even these do not show such a denticle.

The crown is a compressed cone bearing a well developed antero-posterior carina. There is no discernable dentic. post. The labial face shows very weak cr. rug. and only at the posterior part is there other poorly developed sculpture: the crown shows weak undation here.

The lingual face is slightly concave in profile, and bears strong cr. rug. These are fully visible only at the posterior part because only a small portion of enamel remains on that face, but the striations have left distinct traces on the underlying dentine. The cr. rug. arise from a smooth cingulum 1·5 mm wide.

The root is slightly compressed at the base of the crown and is a little tumid below this; this also is a character more or less developed in anterior teeth of squalodontids, but often also (less pronounced) in posterior teeth, for which the term "Basiswulst" (Rothausen 1965: p. 27) or "basal swelling" has been proposed. It may be that the teeth were implanted that far in the connective tissue. The root then narrows and becomes almost cylindrical. About 5-7 mm above the end there is a "sharp" bend, and the lingual side veers labial. There is a slight but distinct constriction 3 mm from the end. On the anterior side, a shallow groove extends from the open end of the root to the constriction.

The position of this tooth is very uncertain. Because enamel is broken away at the lingual side of the crown there is only a possible vestige of a ram. sec. (Fig. 1B) at the denticle. If this were the case it would be an upper right tooth. There is some similarity with B^{1-2} in European squalodontids, but in far smaller dimensions. The development of a dentic. ant. on a tooth anterior to $B^{5}/_{5}$ is however of generic significance.

DISCUSSION

Hall (1911), making some invalid assumptions based on Sanger's rather inadequate description and figure, concluded that the faces of the lost teeth were smooth, and that a tooth from Mt. Gambier (Hall 1911: pl. 36, Fig. 6), possessing a nearly complete root with fangs confluent for most of their length, was of the same species. This latter tooth, however, has the faces strongly ornamented with papillated cr. rug. Hall had disregarded this feature erroneously as being nontaxonomic, and based his two genera on the characters of the incomplete roots (1911: p. 262), which are of far less or even of no importance in this regard.

Kellogg (1923: p. 20) suggested the Mt. Gambier specimen was in reality closer to *Parasqualodon ? wilkinsoni* (McCoy 1867); this was tentatively endorsed by Flynn (1948: p. 186), but it certainly differs in habitus and some very significant points: (*a*) the apical angle is far smaller (40·5°) than in a buccal tooth (P8446.4) of similar position (>47°) of *M. harwoodi*. (*b*) the characteristic number of cr. rug. should be taken at a B^7 (see Appendix 1), but one may be sure that, according to Hall's figure where the cr. rug. are much coarser, the characteristic number of this tooth is far smaller than in *M. harwoodi* (14-15 in the holotype).

These differences clearly distinguish the Mt. Gambier tooth of Hall (1911: pl. 36, Fig. 6) from *M. harwoodi*, and we are sure that this tooth should be consequently included in *Prosqualodon davidi* Flynn because almost the same differences are found between the teeth of *P. davidi* and *M. harwoodi*.

The holotype of *Parasqualodon ? wilkinsoni* (McCoy 1867) itself (Hall 1911: pl. 36, Fig. 5) is similar in shape to the penultimate lower buccal of *P. davidi*. But we hesitate to include *P. ? wilkinsoni* (only the holotype remains in this genus and species) in *P. davidi* without comparing the material itself, since even Flynn accepted this taxon, and indeed there are some differences. We are in doubt whether the form, separation and kind of connection of roots are of any special taxonomic meaning. The occasional appearance of a third, lingual vestigial root (Flynn 1948: p. 183) in *P. davidi* is also of no taxonomic value, because this feature appears in most species of *Squalodon* Grateloup, 1840 with irregular variability in the cheek teeth behind the B^5. (Note, however, Climo and Baker (1972). The real third root they describe in lower cheek teeth of *Austrosqualodon* does seem to be of taxonomic value at least at the generic level.) But there are some other differences in the crown: in *P. davidi* only the anterior carina is convex in lateral view, while in the holotype of *P.* ? *wilkinsoni* it looks as if the posterior one also is convex. All comparable buccal teeth of the Tasmanian form bear three dentic. ant. while the tooth of *P.* ? *wilkinsoni* only bears two but with some spacing, as in *P. davidi* and in the species of *Squalodon*. The cr. rug., as far as it is possible to interpret from the figure of Hall (1911: pl. 36, Fig. 5), are finer and their characteristic number is larger than in *P. davidi*.

All these differences however, compared with the differences between teeth within other squalodontoid genera, seem not to be of generic significance, and it is more likely that this Mt. Gambier tooth represents only another species of *Prosqualodon* Lydekker 1893. Because the material is poor, and because there was no opportunity to compare the material itself, we cannot decide this question here finally, but the existence of the genus *Parasqualodon* Hall 1911 is questionable. An isolated tooth (AUGD T857) figured by Hall (1911: pl. 36, Fig. 4) as *P. wilkinsoni* was regarded by Flynn (1948) to be *Prosqualodon davidi*.

Thenius (1959: pp. 272-273) even united the Tasmanian species with the Australian one, including both under "*Parasqualodon wilkinsoni*". But even if he were right—which seems possible—the IRZN would require this species to be named "*Prosqualodon wilkinsoni* (McCoy 1867)".

Like *S. gambierensis* Glaessner, 1955 (the genus is not entirely certain) *M. harwoodi* has dentic. ant. and post. well-defined, large, sharp-pointed, and smooth-faced. In contrast, the denticles of *P. davidi* are short, obtusely pointed, thick, less well-defined, and bear on their own carinae a varying number of small nod. sec. But this last character occurs in most of the European longirostral Squalodontidae and seems not to be of special taxonomic significance.

In superficial ornamentation, *Metasqualodon* stands between the relatively smooth-faced *S. gambierensis*, and the rough-faced teeth of *Parasqualodon* ? and *Prosqualodon davidi* which are both—somewhat differently—covered with papillated cr. rug. (see Fig. 3 K-N).

What is the taxonomic significance of the ornamentation of teeth with syst. cr. rug.?

The cr. rug. are only of a very limited importance in this regard, but it seems that beside a specific character, they show some general tendencies. For example, Middle Oligocene European Squalodontoidea have characteristic numbers of cr. rug. of about 7, as is also the case for the Upper Oligocene *Microcetus ambiguus* (Meyer 1840). Other Upper Oligocene European forms which are to be placed within Squalodontidae have characteristically 8-10 cr. rug., while most species of Miocene *Squalodon* show 10 and more. *Prosqualodon davidi* and *P. australis* Lydekker 1893 show characteristic numbers of about 7, which seems to be a primitive character, like other features of the teeth of this genus (small apical angle, good symmetry of crowns, three dentic. post. only, ID about 27-28 per cent). The same is the case with early Oligocene squalodontoid buccal teeth described from Oamaru, New Zealand by Keyes (1973). There is a characteristic number of 6-7 with relatively weak cr. rug. (beside this: good symmetry of crowns, three dentic. ant. and post., ID about 25 per cent and only a big apical angle as a specialised character similar to the manner in *Xenorophus sloani* Kellogg 1923).

It should be noted that Keyes apparently did not realise that Rothausen's systematic concept is one of stages and not of clades. Therefore it is highly likely that the early paths of evolution of Squalodontidae and other odontocetes are embedded in the more primitive agorophiid stage, so far known only from such specialised forms as those from the Oligocene upper part of the Jackson Group of South Carolina (Cooke and MacNeil 1952: p. 27). This part, the Cooper Marl, from which the cetacean fossils have been collected, has now been extended into the Upper Oligocene (Whitmore and Sanders 1976: p. 308), on the basis of new studies of the invertebrate fauna. Numerous odontocete skulls have been found there over the past five or six years. Complete skulls of *Xenorophus sloani* Kellogg 1923 have verified conclusions by Rothausen (1965: p. 652) based on the holotype fragment, that it belongs not to the Agorophiidae but must be classed as "incertae sedis" at this time. (pers. comm. to K. R., from Albert E. Sanders, Charleston, June 1976; Whitmore and Sanders 1976: p. 310).

The teeth described by Keyes can only be placed in the superfamily Squalodontoidea with our present knowledge, and thus Keyes in his comparisons (1973: p. 384, 385) is correct only in his opinion that the teeth cannot be placed in *Prosqualodon*, *Parasqualodon*, *Microcetus* (contrary to Keyes, buccals are furnished with dentic. ant.: Rothausen 1961) or *Metasqualodon*.

Concerning the intensity of development of cr. rug. in squalodontoids, there is a difference between Oligocene Squalodontidae and other Oligocene Squalodontoidea. There are very pronounced cr. rug. in the older Squalodontidae with a tendency to become weaker to varying degrees in Miocene forms. But there are only weak cr. rug. in many other Oligocene Squalodontoids—most Middle Oligocene and small forms—as far as we know them at present from material or useful figures. These latter seem to offer more similarity, for instance, with *Neosqualodon* Dal Piaz 1904.

In all these characters *M. harwoodi* resembles very much the Aquitanian species of *Squalodon*, as well as in the high number of 6 dentic. post. (including dentic. bas.), the loss of symmetry in lateral view, and the small ID.

Six dentic. post. is the highest number found in Squalodontidae, known in *Squalodon* only very rarely in B[9, 10] (*S. bellunensis* Dal Piaz 1916; variability left/right:6/5, Rothausen 1965: p. 316). Three dentic. post. for B in middle and posterior positions are characteristic for a relatively ancestral stage in the evolution of squalodontoids. In one lineage of species of *Squalodon*, 1-2 (3) dentic. post. were added later (*catulli*—group: Rothausen 1968: p. 91) in connection with longitudinal stretching of the crown, resulting in a larger apical angle, bending of basal parts of post. cr. rug. in a posterior direction, loss of symmetry in lateral view, straight instead of convex posterior carina, and smaller ID. (In European Oligocene Squalodontidae, ID is 23-27 per cent; in the Miocene the ID of the more conservative *bariensis* group of *Squalodon* is 20-23 per cent, while in the *catulli* group: less than 20 per cent is normally indicated.)

Glaessner (1972) redescribed *Squalodon* ? *serratus* Davis 1888. After a new preparation of the single buccal tooth that represents the holotype, he was able to show that Hall (1911) and Flynn (1948: p. 186) were wrong when they thought this form possibly belonged to *M. harwoodi*, or that both were *P. wilkinsoni*. Rothausen (1965: p. 660), expressing some doubt, had seen in the figure of Davis (1888: Fig. 9) at least some similarity with *M. harwoodi*. Glaessner clearly showed it had a form of its own, but doubted whether it belonged to the genus *Squalodon*. We are sure now that this taxon should be placed in a group with *Prosqualodon*—*Parasqualodon* ?—*Squalodon*? *andrewi* Benham 1942 and has nothing to do with *Kekenodon onomata* Hector 1881 which Kellogg (1923: p. 27) had already placed outside the Squalodontoidea.

All these facts mentioned above make it seem very likely that *M. harwoodi* belongs to another group with *Squalodon*—*Phoberodon* Cabrera 1926—*Squalodon*? *gambierensis*.

The fact that most teeth of *M. harwoodi* agree more with the teeth of longirostral squalodontids than those of brevirostral forms, as far as we know them, need not mean that it represents a longirostral taxon. It may be that these are teeth of a brevirostral species in which the dental evolution has reached a level similar to some Aquitanian *Squalodon* species in the northern hemisphere, but as yet unrepresented by complete skulls. The above-mentioned view has support in some aspects of the anterior buccal teeth of *M. harwoodi*, such as denticles on the most anterior B or curvature of crowns and roots of these anterior teeth.

It should be mentioned that while the teeth of both good species of *Prosqualodon*, *P. davidi* and *P. australis*, show primitive characters, in skull morphology they differ in similar manner as *Eosqualodon* Rothausen 1968 and *Squalodon* Grateloup 1840 (Rothausen 1965: pp. 552, 560); the taxonomic consequences should not be decided here.

One should mention in this connection, as did Rothausen (1965: p. 763), that as in the Equidae, where modern equine characters are combined in different ways with ancestral ones (Tobien 1960: p. 581), so there are here such character pairs in different combinations in Squalodontidae (here considering the buccal teeth only): symmetry/asymmetry; original number of denticles/increased number; relatively big denticles/relatively small ones; coarse cr. rug./weak cr. rug.; vestige of third root/no vestige, etc. There must be similar split lines of evolution, but our knowledge of the Squalodontoidea is far inferior to that of the Equidae. Thus it is still nearly impossible to fix the position and taxonomic state of isolated squalodontoid teeth if the species is not also known by complete or near complete dentitions and skulls. Rothausen in his revision therefore prefers to name such finds in open nomenclature which, however, is not possible if there is already a valid name, such as *Metasqualodon harwoodi* (Sanger 1881).

As mentioned by Keyes (1973: p. 381), the numerous different very early squalodontoids in the southern hemisphere (see below; also new discoveries in New Zealand, pers. comm. R. E. Fordyce, Christchurch, 1975, 1976) have so far been studied much less than those in the north. A revision of this material, as is now being done for a part by Fordyce, may help us to recognise clades as a base for a vertical classification system of the early Odontoceti. This will be the more significant, as brevirostral squalodonts are so far known only from the southern hemisphere, and it is very likely that most modern odontocetes are derived from this group.

STRATIGRAPHY

Sanger (1881: pp. 298-299) reported the following macro-fossils as coming from the same beds as the teeth: (p. 298) "*Echinus, Spatangus, Clypeaster, Pecten, Turritella, Corbis,* and *Spondylus*" and (p. 299) "*Lamna elegans, Notidanus primigenius, Carcharodon angustidens, Nautilus (Aturia) zic-zac, Pecten Poulsoni, Crassatella alta,* and *Clypeaster (Mortonia) Rogersi*". The latter group he interpreted as typically Eocene in age, according to the state of knowledge at that time. His passing description of the source being "in a bed of yellow calcareous clay" fits many of these fossils which may be equated with Miocene species from the Mannum Formation, a sequence of yellow sandy limestones and marls. However, it is at variance with the state of preservation of the teeth, and with their accompanying label. The teeth of *Metasqualodon* are black. The rare shark teeth from the Mannum Formation are ferruginised pinkish- or orange-brown. If the label is interpreted correctly, the teeth came from a depth of 100 feet (about 33 m), presumably in a bore or well. It must be admitted that the only direct evidence for this is the note "100f" on the label. However, considering the rarity of fossil whale material, the fact that the teeth seem to form part of a sequence, mainly from one jaw, and the absence of any bone, the discovery of *Metasqualodon harwoodi* during the sinking of a bore (rather than a well) seems rather likely. The boring method would explain the damaged teeth and loss of such a large part of the specimen. Such discoveries are by no means unknown—several teeth and fragments of a marsupial were recently found at a depth of some 30 m in a bore in New South Wales (Pledge, in prep.). If the *Metasqualodon* teeth were found in outcrop, their preservation would indicate that a more-or-less complete jaw or skull should have been discovered, and it was not. The possibility of such a jaw having disintegrated before discovery does exist, but the teeth show no sign of erosion.

A search through available records of the period has failed to produce any information on such a bore. Two old wells of c. 1880 vintage are known (Hundred of Brinkley, Sections 78 and K[1]) but both are abandoned and full of sand, and nothing is known of their depths or stratigraphy. Another bore in the area (Knight's Bore, Section 217, Hundred of Brinkley, completed 1899) was accurately logged. In this bore, the interval around 100ft. was well within the Oligocene Ettrick Formation (O'Driscoll 1960: p. 230).

The shark tooth (SAM P10867) mentioned on the original label was relocated by one of us (N.S.P.) recently. It seems referable to *Hexanchus agassizi* (Cappetta 1976) although larger. It has a similar preservation to the *Metasqualodon* teeth—dark grey to black—which is typical of bone and teeth from glauconitic or other reducing sediments. The label with the tooth gives the additional information: "R. Murray Cliffs near Wellington".

The beds Sanger (1881) describes would seem to be part of the Mannum Formation (see Ludbrook 1961). This forms a large part of the cliffs at Tailem Bend, only 14 km upstream from Wellington, but it disappears from outcrop only a few kilometres downstream, having been stripped off and replaced by the Pliocene Norwest Bend Formation, a yellow calcareous sand unit with abundant bivalves (notably *Ostrea*, with *Spondylus* and various pectinids). Some of Sanger's assemblages could conceivably have been derived from this younger formation. It is in this same area, just south of Tailem Bend, that the Ettrick Formation makes one of its few surface appearances, as a hard, pale greenish-grey, finely glauconitic marl (Ludbrook 1961: p. 38), occurring as a bench at present pool level of the river. This pool level is largely artificial, following the installation of barrages at the mouth of the river, in the 1930's, to control depth and salinity. It is therefore probable that the extent of outcrop of the Ettrick Formation was far greater *circa* 1880. Being glauconitic, and therefore of a somewhat reducing origin, the Ettrick Formation would yield teeth of a decidedly dark grey-black colouration.

Interestingly, a tooth of the Oligocene shark *Carcharodon angustidens*, collected at Tailem

Bend in 1936, has the same dark preservation as the *Metasqualodon* and *Hexanchus* teeth, and other shark teeth from reducing sediments, and adds support for the provenance of *Metasqualodon* being the Ettrick Formation.

The conclusion is that, whatever the source of the invertebrates allegedly associated with them, the teeth of *Metasqualodon* were obtained from the Ettrick Formation, either in a bore or well or from outcrop. The top of this unit is believed to be equivalent to the end of the Oligocene (Ludbrook 1973: Table 1). Hence the age of *Metasqualodon harwoodi* (Sanger 1881) is Late Oligocene, possibly even Latest Oligocene, since it probably came from near the top of the formation. The younger age is also indicated on the basis of the form of the teeth in relation to the general tendencies and similarities seen in Lower Miocene species of *Squalodon* in Europe.

ACKNOWLEDGEMENTS

We are grateful to Emeritus Prof. M. F. Glaessner for bringing the material to our attention and arranging our collaboration, and also for critically reading the manuscript. Mr. J. M. Lindsay gave advice on certain stratigraphic matters. Mrs. L. Blesing drew figures 1 and 2. Mrs. J. Murphy and Miss F. Gommers typed the manuscripts.

REFERENCES

Abel, O. 1913. Die Vorfahren der Bartenwale. *Denkschr. Akad. Wiss., Wien, math.-nat.* Kl. **90**: 155-224, 12 pl.

Benham, W. B. 1935a. A Reptilian Jaw from Kakanui, South Island, New Zealand. *Trans. Proc. R. Soc. N.Z.*, **65**. 232-238.

Benham, W. B. 1935b. The teeth of an extinct whale *Microcetus hectori* sp.n. *Trans. Proc. R. Soc. N.Z.* **65**. 239-243, 2 pl.

Benham, W. B. 1937. Fossil Cetacea of New Zealand, III. The skull and other parts of the skeleton of *Prosqualodon hamiltoni* sp.n. *Trans. Proc. R. Soc. N.Z.* **67**: 8-14, 4 pl.

Benham, W. B. 1942. Fossil Cetacea of New Zealand. V. *Mauicetus*, a generic name substituted for *Lophocephalus* Benham. *Trans. Proc. R. Soc. N.Z.* **71**: 260-270, 4 pl.

Brandt, J. F. 1873. Untersuchungen über die fossilen und subfossilen Cetaceen Europas. *Mem. Acad. Sci. Saint-Pétersbourg.* **7**, Ser. 20, 372 pp., 34pl.

Cabrera, A. 1926. Cetáceos fosiles del Museo de la Plata. *Revista Mus. La Plata.* **29**: 363-411.

Camp, C. L. 1942. Ichthyosaur Rostra from Central California. *J. Paleont.* **16**: 362-371, 2 pl.

Cappetta, H. 1976. Sélaciens nouveaux du London Clay de l'Essex (Yprésien du Bassin de Londres). *Geobios*, **9** (5): 551-575. 4 pl.

Carter, A. N. 1958. Tertiary foraminifera from the Aire district, Victoria. *Bull. geol. Surv. Vict.*, **55**: 1-76.

Chapman, F. 1918. Descriptions and revisions of the Cretaceous and Tertiary fish-remains from New Zealand. *Palaeont. Bull., Wellington*, **7**: 45 pp., 9 pl.

Climo, F. M. and Baker, A. N. 1972. A new Shark-toothed Dolphin (Cetacea: Squalodontidae) from the Upper Oligocene of New Zealand. *J. R. Soc. N.Z.* **2** (1): 61-68.

Cooke, C. W. and MacNeil, F. S. 1952. Tertiary stratigraphy of South Carolina. U.S. Geol. Survey, Prof. Paper 243-B, 19-29.

Dal Piaz, G. 1904. Neosqualodon nuovo genere della famiglia degli Squalodontidi. *Mém. Soc. Paléont. Suisse* **31**: 1-21.

Dal Piaz, G. 1916. Gli Odontoceti del Miocene Bellunense. II. Squalodon. *Memorie Ist. geol. miner. Univ. Padova* **4**: 94 pp., 10 pl.

Davis, J. W. 1888. On fossil fish-remains from the Tertiary and Cretaceo-Tertiary formations of New Zealand. *Sci. Trans. R. Dubl. Soc.*, ser. 2, **4**: 1-62.

Dechaseaux, C. 1961. Cetacea. In *Traité de Paléontologie*, J. Piveteau, ed., Masson et Cie, Paris. **6** (1): 831-886.

Dickson, M. R. 1964. The skull and other remains of *Prosqualodon marplesi*, a new species of fossil whale. *N.Z. J. Geol. Geophys.* **7**: 626-635.

Dubrovo, I. A. 1971. Novyi rod kitoobraznykh (*Sachalinocetus cholmicus* gen. et sp. nov.) iz miotsena o-va Sakhalin. (A new genus of Cetacea (*Sachalinocetus cholmicus* gen. et sp. nov.) from the Miocene of Sakhalin Island.) *Akad. Nauk SSSR Paleontol. Inst. Tr.* **130**: 87-103. (Russian).

Fabiani, R. 1949. Gli Odontoceti del Miocene inferiore della Sicilia. *Memorie Ist. geol. miner. Univ. Padova* **16**: 32 pp., 2 pl.

Flynn, T. T. 1920. Squalodont Remains from the Tertiary Strata of Tasmania. *Nature, Lond.* **106**: 406-407.

Flynn, T. T. 1923. A whale of bygone days. *Aust. Mus. Mag.* **1**: 266-272.

Flynn, T. T. 1932. A New Species of Fossil Cetacean from Tasmania. *Geol. Mag.* **69**: 327-329.

Flynn, T. T. 1948. Description of *Prosqualodon davidi* Flynn, a fossil cetacean from Tasmania. *Trans. zool. Soc. Lond.* **26**: 153-196.

Glaessner, M. F. 1955. Pelagic Fossils (*Aturia*, penguins, whales) from the Tertiary of South Australia. *Rec. S. Aust. Mus.* **11**: 353-372.

Glaessner, M. F. 1972. Redescription of the Tooth of an Oligocene Whale from North Canterbury, New Zealand. *Rec. Canterbury Mus.* **9** (2): 183-187.

Grateloup, J. P. S. 1840. Description d'un fragment de mâchoire fossile d'un genre nouveau de Reptiles (Saurien) . . . *Act. Acad. roy. Sci. Bordeaux* **2**: 201-210.

Hall, T. S. 1911. On the systematic position of the species of Squaladon and Zeuglodon described from Australia. *Proc. R. Soc. Vict.* (N.S.) **23**: 257-265.

Hector, J. 1881. Notes on New Zealand Cetacea, Recent and Fossil. *Trans. Proc. N.Z. Inst.* **13**: 434-436.

Jenkins, R. J. F. 1974. A new giant penguin from the Eocene of Australia. *Palaeontology* **17**: 291-310.

Kellogg, R. 1923. Description of two squalodonts recently discovered in the Calvert Cliffs, Maryland, and notes on the shark-toothed cetaceans. *Proc. U.S. natn. Mus.* **62**: 69 pp.

Kellogg, R. 1928. The History of Whales, their Adaption to life in the Water. *Q. Rev. Biol.* **3**: 29-76, 174-208.

Keyes, I. W. 1973. Early Oligocene squalodont cetacean from Oamaru, New Zealand. *N.Z. J. Marine and Freshwater Res.* **7**: 381-390.

Ludbrook, N. H. 1961. Stratigraphy of the Murray Basin in South Australia. *Bull. geol. Surv. S. Aust.* **36**: 96 pp., 8 pls.

Ludbrook, N. H. 1973. Distribution and Stratigraphic Utility of Cenozoic Molluscan Faunas in Southern Australia. *Tohoku Univ., Sci. Rep., 2nd ser. (Geol.), Spec. Vol.* **6** (*Hatai Memorial Vol.*) 241-261, 1 table, pls. 24-28.

Lydekker, R. 1893. Contributions to a knowledge of the fossil vertebrates of Argentina. Cetacean skulls of Patagonia. *Ann. Mus. La Plata. Palaeont. Argent.* **2**: 2-13.

Lydekker, R. 1899. On the skull of a shark-toothed dolphin from Patagonia. *Proc. zool. Soc. Lond.* **1899**: 919-922.

McCoy, F. 1867. On the Occurrence of the genus *Squalodon* in the Tertiary Strata of Victoria. *Geol. Mag.* **4**: 145, 1 pl.

Mahoney, J. A. and Ride, W. D. L. 1975. Index to the genera and species of fossil Mammalia described from Australia and New Guinea between 1838 and 1968. *Spec. Publs. West. Aust. Mus.* No. 6, 1-250.

Meyer, H. V. 1840. Über *Phoca ambigua* Münster. *Beitr. Petrefactenkunde, Graf zu Münster* **3**: 1-7, 1 pl.

Neave, S. A. 1940a. *Nomenclator Zoologicus* **3**: 1-1065.

Neave, S. A. 1940b. *Nomenclator Zoologicus* **4**: 1-758.

O'Driscoll, E. P. D. 1960. The Hydrology of the Murray Basin Province in South Australia. *Bull. geol. Surv. S. Aust.* **35** (2 vols.). 300 pp., 14 charts.

Pritchard, B. G. 1939. On the discovery of a fossil whale in the older tertiaries of Torquay, Victoria. *Victorian Nat.* **55**: 151-159.

Romer, A. S. 1945. *Vertebrate Paleontology* 2nd ed., 687 pp., University of Chicago Press, Chicago.

Romer, A. S. 1966. *Vertebrate Paleontology* 3rd ed., 468 pp., University of Chicago Press, Chicago.

Rothausen, K. 1958. Marine Vertebraten (Odontaspidae, Lamnidae, Sparidae, Dermochelyidae, Squalodontidae) im oberoligozänen Meeressand von Süchteln und Düsseldorf. *Fortschr. Geol. Rheinld Westf.* **1**: 363-384.

Rothausen, K. 1961. Über *Microcetus*, einen kleinen Squalodontiden aus dem Oberoligozän. *Neues Jb. Geol. Paläont. Abh.* **112**: 106-118.

Rothausen, K. 1965. Die europäischen Squalodontidae (Odontoceti) und ihre Stellung zu den übrigen Squalodontoidea, I. Kraniales Skelett. Habilitationsschr., 856 pp., 77 pl., Mainz. (unpublished thesis).

Rothausen, K. 1968. Die systematische Stellung der europäischen Squalodontidae (Odontoceti, Mamm.). *Paläont. Z.* **42**: 83-104.

Rothausen, K. 1970. Marine Reptilia and Mammalia and the problem of the Oligocene-Miocene boundary. *Comm. Mediterr. Neog. Strat. Proc IV, Sess., Bologna* 1967; *G. Geol.* **35** (1): 181-189.

Sanger, E. B. 1881. On a Molar Tooth of *Zeuglodon* from the Tertiary Beds on the Murray River near Wellington, S.A. *Proc. Linn. Soc. N.S.W.* **5**: 298-300.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. nat. Hist.* **85**: 1-350.

Stromer, E. 1908. Die Archaeoceti des Aegyptischen Eozäns. *Beitr. Paläont. Geol. Öster.-Ung.* **21**: 106-178.

Thenius, E. 1959. Tertiär. Wirbeltierfaunen. *Handb. Strat. Geol.* **3** (2): 1-328.

Thomson, J. A. 1905. The Gem Gravels of Kakanui; with remarks on the geology of the district. *Trans. Proc. N.Z. Inst.* **38**: 482-495.

Tobien, H. 1960. Zur Geschichte der pferdeartigen Unpaarhufer im Tertiär Europas. *Z. dt. geol. Ges.* **112**: 580-581.

Winge, H. 1919. Udsigt over Hvalernes Slaegtskab. *Vidensk. Meddr. dansk. naturh. Foren.*, **70**: 59-142.

Whitmore, F. C., Jr. and Sanders, A. E. 1976. Review of the Oligocene Cetacea. *Syst. Zool.* **25**: 304-320.

Zigno, A. de 1876. Sopra i resti di uno squalodonte scoperti nell'arenaria miocena del Bellunense. *Memorie Ist. Ven. Sci. Lett. Art.* **20**: 17-33.

APPENDIX I

STANDARDISED TERMINOLOGY FOR SQUALODONTOID TEETH

Buccal tooth—(*B*). Rothausen (1965: p. 718; 1968: pp. 86, 100) stated that there was no way of determining the premolar—molar division and homology in most squalodontoids and proposed this more neutral term, similar to the sense of Dal Piaz (1916: p. 17) and Kellogg (1928: p. 53). The term is equivalent to the informal "cheektooth" (*bucca*: Lat. cheek) also used herein. Buccal teeth are numbered consecutively from the front, i.e. $B^1/_1$, $B^2/_2$, $B^3/_3$ . . . . $B^n/_n$.

Denticulus anterior; d. posterior—*Dentic. ant.; dentic post.* (*denticulus*: Lat. little tooth, denticle) small conical extensions on the anterior and posterior cutting edges (carinae) of the flattened buccal crowns.

Denticulus basis—*Dentic. bas.* Basal denticle—a small cusp at the base of the crown on the anterior or posterior edges. They have special significance in some cases and therefore are mentioned separately.

Nodulus primus—*Nod. prim.* Small tubercular extensions of the main carina, c.f. *nod. sec.* Both are to be strictly separated from "denticles".

Nodulus secundus—*Nod. sec.* Small tubercle-like extensions on the carinae of denticles.

Cingulum A smooth encircling zone of thickened enamel at the base of the crown.

Crista rugosa—*Cr. rug.* (*crista*: Lat. ridge) Enamel ridges, mostly irregular, that may be more or less covered with enamel papillae.

Systema cristarum rugosarum—*Syst. cr. rug.* Viewing the apical end of a cr. rug. as the stem or trunk, one sees it divide into branches towards the base of the crown. These branches may anastomose with others from the same trunk, but not with those from another "stem". They belong to closed systems. These syst. cr. rug. die out at the cingulum (Fig. 1). This observation seems to be true for all squalodontid teeth.

Undation (*unda*: Lat. wave). Common, weak, relatively broad, longitudinal, wave-form surface relief on the crown face following the curvature of the crown of anterior teeth. (Fig. 1: Rothausen 1965: p. 26, Abb. 4).

Crenelation Minute serration on the carinae of anterior teeth of squalodontids (Fig. 1: Rothausen 1965: p. 26, Abb. 4).

Ramus primus—*Ram. prim.* The main branch of the carina when it divides. (Fig. 1).

Ramus secondus—*Ram. sec.* A weaker, secondary branch at the basal end of the anterior carina in anterior teeth of squalodontids. (Fig. 1).

Apical angle The angle enclosed by lines from the apex to the anterior and posterior end points of the base of the crown; gives an index of the antero-posterior diameter (*a*) to the height of the crown.

Index denticulorum—(*ID*). Expresses the relationship between the basal diameter of the largest dentic. post. (ad), measured in the direction of the carina, and the antero-posterior diameter of the crown (*a*).

$$\text{i.e. ID} = \frac{100\,\text{ad}}{\text{a}} \text{ per cent}$$

For best comparison of species, the ID should be calculated only for B^7 to B^9 (Rothausen 1965: p. 32).

Index basalis—(β). Expresses the flattening of the crown. $\beta = \frac{100\text{b}}{\text{a}}$ where b is the transverse diameter of the crown (above the anterior root in two-rooted teeth).

Cristae density—*Cr. density.* The characteristic number of cr. rug. The number of cr. rug. counted in 5 mm just posterior of the middle of the labial face about 5 mm above the base of the crown, preferably of a B^7.